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AGONISTIC AND COURTSHIP DISPLAYS OF MALE *ANOLIS SAGREI*

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ABSTRACT. Male *Anolis sagrei* perform a dewlap fanning display and four different bobbing displays in agonistic and courtship encounters. Only one of the bobbing displays has a species-specific, stereotyped pattern. The total number of bobs and the number of bobs in each unit of this display and the use of the dewlap showed considerable variability both within and between individuals. The frequency distribution of the type of display used in aggressive encounters showed more inter- than intra-individual variability. Dewlap fanning displays were used at a relatively higher frequency before crests were raised, but the dewlap was used with the bobbing display at a relatively higher frequency by males after the erection of crests. Submissive animals displayed less frequently overall and were more apt to use a dewlap fanning display, but they were less apt to use the dewlap with a bobbing display than a dominant male. Male *A. sagrei* were less apt to use the species-specific stereotyped pattern in courtship than in aggressive encounters. The "jiggle" bob display immediately preceded half of the attempted matings. A dewlap fanning with erect posture was associated with the termination of a copulation.

INTRODUCTION

The brightly colored dewlaps and stereotyped bobbing displays of males of the iguanid lizard genus *Anolis* may communicate information regarding species, sex, reproductive state, dominance and territorial status, intentions, and level of arousal. Dewlap color alone sometimes does not appear to be an important element in species recognition and female choice for the solitary anole *A. carolinensis* (Greenberg and Noble, 1944; Crews, 1975a). However, in a complex *Anolis* fauna, color and dewlap proportions may

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provide redundant information for species recognition (Williams and Rand, 1977). Jenssen's work (1970a) with *Anolis nebulosus* indicates that the male's species-specific bobbing display does indeed play a significant role in sexual selection and female choice.

In examining anoline displays, recent researchers have focused on the degree of stereotypy (the amount and possible significance of variability within and among individuals) and the complexity of display repertoires of different species. Displays may vary either in temporal patterns or by the presence or absence of various components within the display. Species differ considerably in the amount of stereotypy of their displays, and the source of variability may be intra-individual or between individuals (Jenssen 1978). *Anolis carolinensis* (Crews, 1975b), *A. aeneus* (Stamps and Barlow, 1973), and *A. nebulosus* (Jenssen, 1971) have very stereotyped displays. Each individual performs a consistent display, but there is variability between individuals. Different populations of *A. nebulosus* have been examined and still further variability between populations was found. Other species, however, like *A. limifrons* (Jenssen and Hover, 1976) show greater intra-individual variability than inter-individual differences. At the extreme, almost all (97%) of the variability of *A. townsendi* displays is attributable to intra-individual variation (Jenssen and Rothblum, 1977). *Anolis opalinus*, on the other hand, was found to be almost completely lacking stereotypy at any level, individual or population, in that there was no single discrete display pattern. However, 75% of the analyzed displays fit a theme which explained the highly variable bob number and display cadence (Jenssen, 1979).

The complexity of the display repertoire of a species is another important feature. Researchers (e.g., Carpenter and Grubitz, 1961) first described only two basic types of displays, a courtship pattern of rapid head bobs and a species-unique "signature" pattern. The latter type was originally labeled an "assertion" display that, with modifiers, blends into a "challenge" display (Carpenter, 1967; Jenssen, 1970b, 1977; Crews, 1975b). Typically, if other display types were described, they consisted of the signature display plus modifiers (e.g., four-legged push-up posture preceding dewlap fanning), or they may be characterized by a different coordination of the dewlap extensions during the head bob sequence. Recently, researchers have found greater complexity in the display repertoire of some anoles (Hover and Jenssen, 1976; Jenssen and Rothblum,

1977). *Anolis aeneus*, *A. limifrons*, and *A. townsendi*, for example, have several clearly distinct display types which differ not just by the modifiers or the context in which they appear, but also by different bob patterns.

This paper described the display repertoire of male *Anolis sagrei* in agonistic and in courtship situations. A description and analysis of the species-specific stereotyped display and its variable elements are given. An attempt is made to analyze these displays and their modifiers in terms of the social context in which they appear and the effect they have on conspecifics. The possible role of the species-specific signals used in sexual selection is discussed.

MATERIALS AND METHODS

Anolis sagrei has a wide distribution, occurring on Cuba, Jamaica, the Bahamas, Little Cayman, Cayman Brac, Swan Island, and coastal areas of Mexico and Belize, and has recently been introduced into Florida (Williams, 1976). It occupies a relatively open habitat. During the breeding season, males and females are strongly territorial. A male territory has been described by Evans (1936) as at least 50 m² and containing up to three females. In cultivated areas, it is typical for males to occupy a hedge row or fence at approximately 6 m intervals (Evans, 1936; Scott, personal observation).

Twenty males (55–62 mm snout to vent length), 12 females and 8 juveniles were collected near the University of South Florida, Tampa, in May 1979 when the mature males and females were sexually active.

The lizards were held in experimental cages of two designs. In Design 1, one large male, a juvenile male and two to three females inhabited an aquarium 75 cm long \times 32 cm deep \times 45 cm high. Two of these aquaria so arranged were placed end to end with a removable opaque divider between them. Each contained a live plant and a prominent perching branch. The far side of each aquarium was covered by bark which was also favored as a perching site. Thus, when the opaque divider was removed, the two territorial males could see each other but were physically separated by a double pane of glass. In this design, 5 pairs of 10 different males were tested against each other three to five times. In Design 2, a wire cage 47 cm long \times 51 cm deep \times 39 cm high was divided in half

longitudinally by a removable opaque partition. A single large male was housed in each half, which also contained a plant, a perch, and a bark wall. In these cages, the animals were in physical as well as visual contact with each other when the partition was removed. In this design, three pairs of six different males were effectively tested against each other only once since subsequent tests would have been declared "no contest" at the outset by the participants. These wire cages were kept in Sherer-Gillet environmental chambers with transparent doors. All animals experienced a constant environmental regime of 14L:10D photoperiod and a corresponding temperature cycle of 32:23°C. All animals received food (mealworms and crickets) and water *ad lib*. Observation of the aquaria animals in Design 1 was made from behind a cardboard blind to ensure that the displays were directed at conspecifics and not the observer. The animals in the lighted environmental chambers of Design 2 were observed in a darkened room, making the observer relatively inconspicuous. The cages were arranged in each case so that no animal could see a conspecific except those in its experimental setup. When the partition was in place males were only occasionally observed displaying at the juveniles or females. Males were housed individually before they were placed in the experimental cages.

All males were allowed at least one week to acclimate to a new cage before testing was begun. Agonistic tests were at least 15 minutes long and continued 5 minutes after the situation appeared stable (that is, when there was no change in positions and display types used by the two animals). Courtship tests were terminated when the animals finished copulating.

Male agonistic behavior was studied in both types of cage designs with the opaque dividers removed. Males in the aquaria of Design 1 were repeatedly tested against each other whereas those in the wire cages of Design 2, which allowed physical contact, only met once because, once beaten, the subordinate animal did not display but retreated. Courtship behavior was observed only in the cages of Design 2; the partitions were left intact and a female was introduced into a wire cage which housed a single male.

Parameters of male behavior were recorded with a 10 channel Esterline Angus operation recorder Model A. Displays were taped with a Sony video camera AVC 3210 with a 75 mm f12.5 lens and analyzed with a Sony videorecorder AV 3650 with which the tapes

could be slowed to 8% actual speed. The head and dewlap movements were transcribed onto a strip of acetate by running the acetate in front of the video screen at a constant known speed, using the gears of the event recorder and following the action with a felt tipped pen placed on the rostrum of the videotaped lizard. The time framework could be superimposed on the tracing making corrections for the video recorder speed and the gear ratio of the event recorder. Only animals from the wire cages of Design 2 were videotaped because the T.V. equipment was less conspicuous to the subjects.

A total of 620 agonistic displays by 12 different males were observed in 18.8 hours. Two hundred twenty-nine displays of eight different courting males were observed in 12.4 hours. Thirty-one displays of three males in two entire agonistic events and three different males in entire courtship tests were taped and analyzed. Recording data on the video equipment and event recorder provided different benefits. When using the event recorder, the social context of the display and the response of the recipient could easily be included. In this way the meaning of the display could be defined by the response it provoked. With the video equipment it was possible to record data on the modifiers of the displays in fine enough detail to compare and discuss variability within and between individuals. The cadence of bobs could also be recorded to discriminate the type of bobbing display and to relate it to the social context.

For purposes of discriminating dominant and submissive behavior, the animals of all the tests in both cage designs were divided into two groups on the basis of their behavior at the end of the test. An animal was judged to have been acting dominant throughout the test if he was still facing his opponent at the end with an alert posture. Those anoles that ran from their opponent to the far side of the cage and had a posture low to the substrate were classed as submissive for the whole test. Since these classifications were somewhat subjective, borderline cases in which either animal showed a mixture of dominant and submissive behavior at the end of the test were not used in the following analysis. Within each group there was little variance in the frequency of each type of display performed (Table 1); therefore, for statistical purposes, data from all dominant males were pooled, as were those from all subordinate males.

Table 1. Frequency \pm variance of displays by type per minute of animals judged at the end of the test to be dominant or subordinate.

	Dominant animals (N = 34)	Subordinant animals (N = 11)	Difference
Dewlap only	0.07 \pm 0.01	0.07 \pm 0.01	n.s.
Bob only	0.43 \pm 0.06	0.21 \pm 0.04	t = 2.70, p < 0.01
Bob + dewlap	0.16 \pm 0.02	0.01 \pm 0.00	t = 3.49, p < 0.001

Any encounter escalated (if it were going to) in a predictable fashion. Modifiers were added to displays and other behaviors appeared in the same order each time, as the states of arousal of the participants increased and their bodies became more tense. To facilitate analysis of behaviors and responses in agonistic encounters, confrontations were divided into three stages which were differentiated by changes of body posture. In the first stage, a male had not yet erected either a nuchal or dorsal crest or laterally compressed his body and was said to be in state A. In the second stage, a male had both crests (state B) and in the third, most aroused stage, he had laterally compressed his body as well (state C).

Statistical tests used were t-test of proportions, arcsin transformed, to test the difference between the means of two samples and a one-way analysis of variance to examine the inter- and intra-individual variance in display stereotypy. Means are expressed \pm the standard error.

RESULTS AND DISCUSSION

Displays and Modifiers

A display is a sequence of behaviors, usually performed in its entirety, which communicates information about the sender. In the following context, it refers to the change in amplitude over time of a lizard's head and/or dewlap and encompasses any consistently associated stereotyped movements or postures. A modifier is a posture (static modifier) or movement (dynamic modifier) which is not always present with a particular stereotyped display but may be added (Jenssen, 1978). *Anolis sagrei* sometimes performed these modifying behaviors, particularly postures, separately from stereotyped head bob displays.

A brief description of the displays investigated follows. The frequency distributions of the display types, degree of stereotypy,

and information conveyed are all discussed later in the context in which the display was used.

Dewlap Fanning. The dewlap, which in Florida *A. sagrei* is bright orange with a yellow margin, is extended by the hyoid apparatus. The pattern and context of this action is extremely variable. It can occur as a single extension or in a fast or slow series of as many as 15 separate extensions. The series have no discernible pattern, and the display is used in all observed contexts and may be directed at a human observer as well as a male or female conspecific.

Bobbing. The head can be bobbed from the neck, from mid-body, or as a four-legged push-up. Bobs from the neck or mid-body can occur singly or in a series of a single posture, or the display may begin as bobs from the neck and finish as bobs from the mid-body. These postures may demonstrate increasing states of arousal in that order. Bobs with a four-legged push-up posture are not performed singly. These four-legged push-up bobbing displays are typically 8–10 bobs but may contain 18 to 20 and last as long as 30 seconds.

There are three different sorts of bobbing displays.

(A) *Anolis sagrei* can perform a species-specific stereotyped display which has a distinctive cadence to a series of bobs which may be called its "signature" display (Stamps and Barlow, 1973). It consists of four units: 2 quick initial bobs of increasing amplitude, a long bob, a short bob, followed by a series of 3 to 12 even-tempo bobs dampening in amplitude (Fig. 1). There may be variation in bob number of any unit of the pattern. If the dewlap is extended during the display, it always flashes on the third (long) bob and variably during the dampening series of bobs at the end. This signature display occurs in an assertion context (i.e., non-directed or low conflict situation), in both agonistic and courtship tests, and at every state of arousal.

However, sometimes this bobbing display does not consist of this characteristic pattern. It may, however, have some similar elements to the signature pattern such as a long bob accompanied by a dewlap extension followed by a short bob. These displays also may or may not be accompanied by dewlap extensions and without them as a marker, the elements similar to the signature pattern often could not be identified. For example, in the display illustrated by Figure 2, the dewlap extension at 5 seconds marks what might be the long bob followed by the short bob characteristic of the signature pattern but it is unrecognizable by the pattern of bobs alone. These displays also may occur in any context.

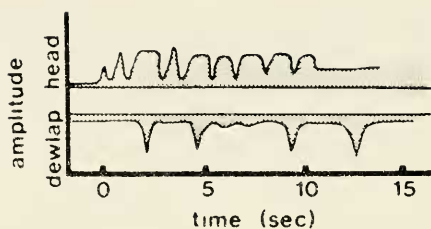


Figure 1. The signature display of *Anolis sagrei*.

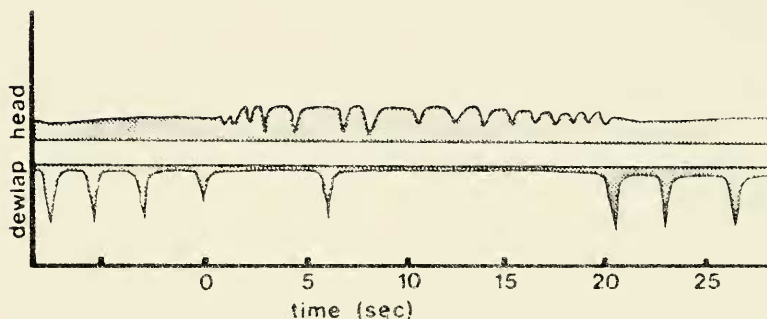


Figure 2. A typical example of a display that did not fit the signature pattern.

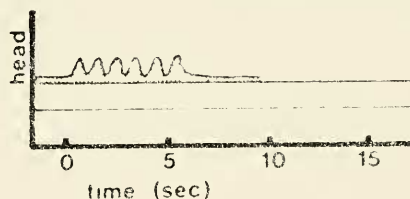


Figure 3. The quick rhythmic bobbing display.

(B) The second bobbing display is characterized by a quick (about 1-2/sec) rhythmic bobbing with no inter-bob pause and without any dewlap extension (Fig. 3). The amplitude of these bobs was less than that of the bobs of the signature display, and usually it was performed with the head and body close to the substrate. In these tests, 49 of 53 times it was performed by an animal in a submissive situation. However, it was occasionally (4 times)

performed by a highly aggressive dominant male in a context when the opponent had a submissive posture.

(C) The third type of bobbing display is jiggling action of the head. The amplitude of these bobs was very much less than that of other bobbing displays and the rate was much faster (8–10/sec). In these tests, all 34 times this display was used was in courtship situations and was performed by the male usually as he approached the female to take a neck grip prior to mating. It may be performed as a separate display or tacked on to the end of another.

Modifiers. Many different behaviors may be used to modify a display. Some were consistently used in a particular context and state of arousal and often caused a consistent response in the recipient and therefore these modifiers may impart specific information on the intent and motivation level of the animal displaying. See Table 2 for a list of modifiers frequently used, their social context, and state of arousal when used.

Male-Male Encounters

The encounters between two males were staged such that they would both be expected to act territorially. A total of 12 different males were used in 26 tests. In Design 1, the two aquaria which each housed resident males were sufficiently large that the males were often 150 cm apart when they first saw each other, so that in 45% of the 25 tests they escalated aggression (see below) and were only prevented from combat by the glass partitions. When these same two males confronted each other in future tests, both continued to act aggressively. The situation in the wire cages of Design 2 was different. The animals were less than 50 cm apart when they first saw each other, and there was no physical partition. In every instance the rank order of the two was quickly apparent when one male fled without a contest; there was no escalation of aggression. The physical proximity seemed to be a deterrent to bluffing by the less aggressive male and did not allow for a slow escalation of aggressive behavior and evaluation of each other.

The sequence of events in an escalating fight is typical of that described for other anoles (Crews, 1975b). Behaviors and modifiers to displays are added in a sequence that is predictable. In a aquaria of Design 1, males would display towards each other with first a nuchal crest and then a dorsal crest being erected. The whole body

Table 2. Modifiers used in displays of male *A. sagrei* and their context. The steps in escalation of an encounter from first display to conclusion (combat or neck grip) were consistently ordered (see text). The state of arousal refers to the stage of escalation.

Modifier	Display	Context	State of Arousal
Dewlap extension	Signature display	Assertion, courtship & aggression	All
Nuchal crest	Signature display or continued condition	Aggression	Moderate
Dorsal crest	Signature display or continued condition	Aggression	Mod. high
Lateral compression	Signature display or continued condition	Aggression	Highest
Engorged throat	Usually a continued condition but can accompany signature display instead of dewlap extension	Aggression	Moderate → highest
Tail lift	In 4-legged push-ups of signature display	Courtship & aggression	Mod. high → highest
Tail lash	Alone or with signature display	Aggression	Mod. high → highest
Tongue protrusion	Alone or with signature display	Aggression	Mod. high → highest
Lip smack	Alone or with signature display	Aggression	Moderate → highest
Slow approach	Jiggle display	Courtship	Highest

can then be laterally compressed. (Table 3 illustrates that these successive posture changes indicate increasing states of arousal.) As the lizard's body becomes more tense, the bobbing action becomes more exaggerated, from nods to two-legged push-ups to four-legged push-ups. At this point increasing intensity of arousal is signaled by behaviors other than the bobbing displays. The males approach each other either slowly or with a rush. They will orient head to tail, lunge, and threaten by gaping their mouths. Because the animals were either physically separated or unwilling to engage in combat, no staged fight in either Design 1 or 2 proceeded past this point, but in a natural setting the fight will end with jaw grappling and one being physically pushed off the branch and chased off (Scott, personal observation).

Table 3. The probability of an animal in an agonistic confrontation taking a more aggressive posture. A, B, and C are the states of arousal, and $A \rightarrow B$ is the probability of a male in the first state going to the second. An animal in state A has a body posture without nuchal or dorsal crests or lateral compression of the body. An animal in state B has both crests and one in state C has crests and lateral compression.

	# tests	$A \rightarrow B$	$A \rightarrow C$	$B \rightarrow C$	$C \rightarrow B$	$C \rightarrow A$	$B \rightarrow A$
Dominant animals	34	0.91	0.09	0.74	0	0	0
Submissive animals	11	0.45	0	0.27	0.09	0.18	0

Twenty-four displays by males clearly acting territorially were taped and analyzed; all had some recognizable components of the signature display. There was however a great deal of variability. Five of seven displays by one male, and four of five by another, were of the signature pattern. The remaining displays for these two animals were varied by having either one or three quick initial bobs instead of two. The third male whose displays were taped had only three of 12 showing the signature pattern. The number of initial bobs (2, 3, or 4), slow bobs (1 or 2), and quick bobs (0, 1, or 2) varied so that for some displays the signature pattern was barely recognizable. The mean number of bobs in these filmed displays was 11.1 ± 0.4 . The mean time elapsed was 17.4 ± 0.8 seconds. The coefficients of variation for the number of bobs in these variable units of the signature display in these agonistic encounters are: 24% for the initial bobs, 32% for the slow bob, 40% for the quick bob, and 23% for the total number of bobs in the display. Twenty of these 24 taped displays were accompanied by dewlapping, whereas only 23% of the bobbing displays included dewlap extensions in the total sample of all displays observed. Twenty-two of the taped bobbing displays were two-legged push-ups with crests erected; in 12 displays the body was laterally compressed as well, as the state of arousal during the confrontation increased. Each of the three animals gave one or two displays that began as four-legged push-ups, usually raising the tail on the up stroke of the bob (Fig. 4), and dampened to two-legged push-ups. Tail lifts were used as a modifier of two-legged push-ups in conjunction with nuchal and dorsal crests three times and once with lateral compression as well. One display which included crests and lateral compression also was accompanied by a tongue protrusion and a lip smack.

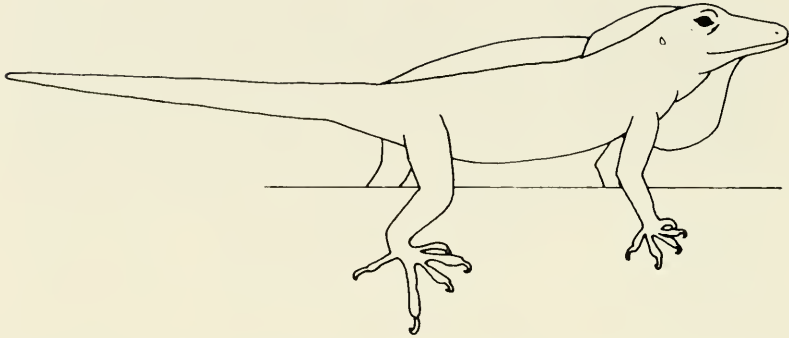


Figure 4. Aggressive display with a 4-legged push-up, nugal and dorsal crests, lateral compression of the body, and a tail lift.

Information on the context of each display type was gained by pooling the data from all the staged encounters in both cage designs and examining the frequency distributions of display types (dewlap flashes, bobbing displays, and bobbing displays with dewlap extensions). Four bobs and dewlap flashes in a continuous sequence were arbitrarily chosen as the minimum to constitute a display. The mean proportion of dewlap fanning displays of all displays was 0.14 ± 0.02 . There was little intra-individual variation in the proportion of use of this display form from one test to another. In a one-way analysis of variance, 87% of the variation in the frequency of use of this display type was between individuals and 13% between tests of a single individual ($F = 7.28$, $p < 0.01$). This tendency was enhanced by the fact that each male in the cages of Design I was always matched against the same opponent and most animals responded in a characteristic fashion in each test. The frequency with which a bobbing display was accompanied by dewlap extension was similarly consistent. Eighty-three percent of the variation was between animals ($F = 4.77$, $p < 0.01$). The mean proportion of bobbing displays with dewlap modifier was 0.23 ± 0.03 (Fig. 5a).

A male was judged to be either submissive or dominant on a test-by-test basis, but he probably performed as both a dominant and submissive individual during the test. Most animals that "lost" ultimately still responded with varying intensity to the challenge of the more aggressive one. In addition, the relative ranks of submission and dominance were not necessarily consistent even

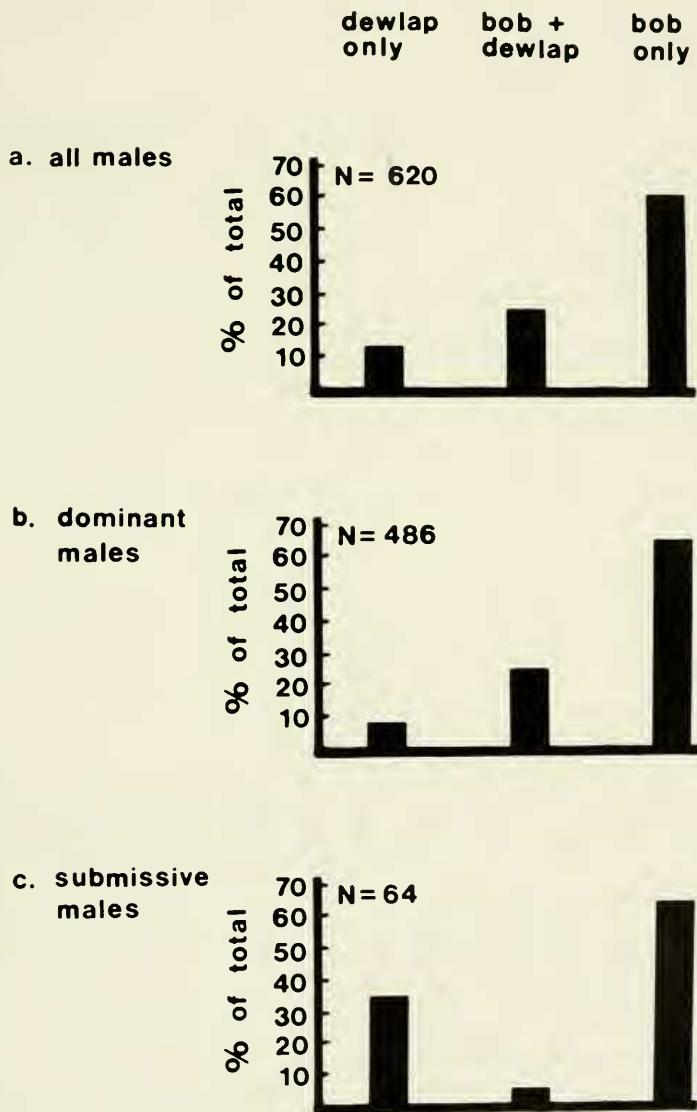


Figure 5. Frequency distribution of display types performed by males in agonistic confrontations. All displays were used in a., but only those by clearly dominant or clearly submissive males were used in b. and c.

when the same opponents were repeatedly matched in the separated aquaria.

Submissive animals displayed (either bobbing or fanning) less than half as often (0.29/minute, $N=11$) as dominant ones (0.63/minute, $N=34$) (Table 1). Dewlap fanning formed a significantly higher proportion of the total displays by submissive animals than by dominant animals ($\bar{x} = 0.34 \pm 0.08$ vs. $\bar{x} = 0.08 \pm 0.01$; $t = 2.29$, $p < 0.05$) (Fig. 5b, c). A significantly lower proportion of the bobbing displays of submissive animals was accompanied by dewlap extensions, $\bar{x} = 0.03 \pm 0.01$, than of dominant animals, $\bar{x} = 0.30 \pm 0.03$ ($t = 3.36$, $p < 0.01$). Therefore, submissive animals use their dewlaps for fanning displays but not to modify bobbing displays. A significantly higher proportion of the bobbing displays of submissive animals were the rapid bob (Fig. 3), $\bar{x} = 0.25 \pm 0.09$ for submissive animals versus $\bar{x} = 0.01 \pm 0.01$ for dominant animals ($t = 2.99$, $p < 0.01$). Dominant animals also took progressively more aggressive postures and reached a higher arousal state more frequently than submissive ones did (Table 3).

The pacing of agonistic encounters varies with each fight, even when the combatants are known to each other. Of the pairs that always escalated to a full confrontation, usually the same individual was faster to be aroused. The mean latency time of aggressive animals for developing nuchal and dorsal crests was 4.6 ± 0.4 minutes ($N=38$) and for lateral compression was 7.4 ± 0.5 minutes ($N=26$). There was a great deal of intra-individual variation in the kind of displays, if any, that were performed before both crests were erected and the body compressed. But the frequency distribution of display types performed in this low arousal state was different for animals that would be judged dominant or submissive at the end of the test, i.e., there were behavioral differences in the two groups from the beginning of the test (Fig. 6).

A display by one male *A. sagrei* often prompted a display by the other in these tests. Forty percent of all displays seen occurred within 10 seconds after a display or single bob or dewlap flash by the opponent, but there was no particular tendency to use the same sort in answer as the one just seen. For example, a bobbing display was followed by dewlap fanning display or a bobbing display. Forty to 50% of the fanning displays and the bobbing displays with and without dewlap modifier of both dominant and submissive animals was in response to the opponents display. There was a slightly

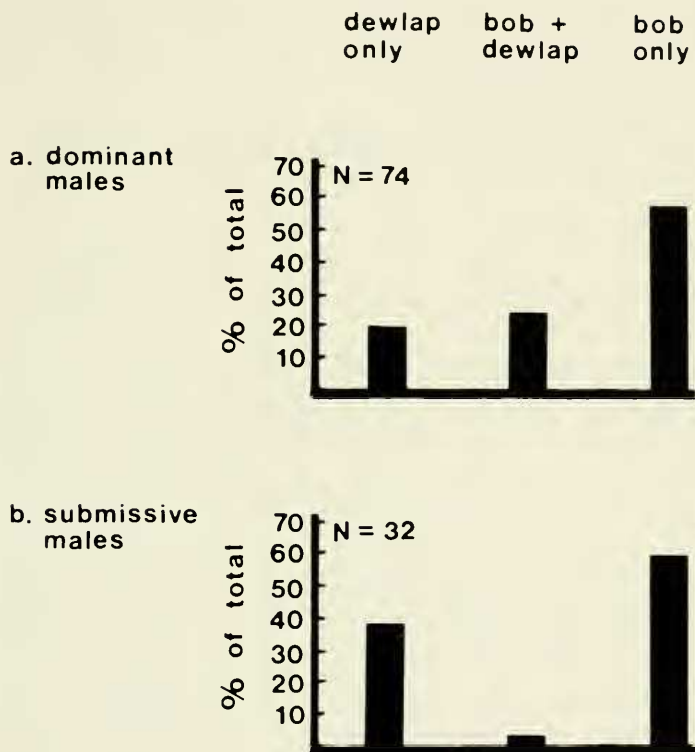


Figure 6. Frequency distribution of display types performed by dominant and submissive animals in agonistic confrontation before nuchal or dorsal crests had been erected or the body had been laterally compressed.

higher tendency for a dominant animal to respond with a bobbing display with a dewlap extension. Submissive animals performed almost no bobbing and dewlap displays, but those few that they did perform were all in response to the opponent's display (Table 4).

Male-Female Encounters

All male-female encounters were staged by introducing a female into the wire cage of Design 2 of a single resident male. Eight different males were used in 33 tests. The pattern of courtship behavior appears to be very similar to that described for other anoles (Noble and Bradley, 1933; Evans, 1938; Crews, 1977). Upon

Table 4. Proportion and number of each type of display for submissive and dominant animals which were in response to a display by the opponent rather than spontaneously performed.

	Total displays	Dewlap fanning	Bobbing displays	Bobbing displays + dewlap
Dominant animals	40% (192)	35% (18)	37% (114)	49% (60)
Submissive animals	44% (28)	42% (8)	40% (17)	100% (3)

introduction of a female, the territorial male performs the dewlap fanning display or the bobbing display with or without dewlap extensions either with the signature pattern or not. The bobbing displays seen in a courtship situation have none of the aggressive modifiers, such as crests and lateral compression, that characterize male-male encounters. The male then approaches the female, sometimes with a jiggling action with his head, takes a grip on her neck, and swings his tail beneath hers, juxtaposing his cloaca to hers and inserting a single hemipenis. More displays may follow mating. It has been reported for other anoles (Crews, 1977) that a receptive female will stand and arch her neck for the male to take a grip. In this study, no female was ever seen to show receptive behavior. In all but two of the 33 tests the male attempted to mate by taking or attempting to take a neck grip on the female. Eleven tests ended in copulation. In four of these, the matings were very short (<2 minutes), and the male maintained his mating posture several minutes after the female escaped, indicating that intromission may not have occurred. Excluding those matings which may have been incomplete, the mean time for intromission was 6.7 ± 0.83 minutes.

The anoline courtship display has been characterized as ending with a series of jiggly bobs (Crews, 1975b). In 18 of 33 courtships observed, *A. sagrei* males also performed a jiggle bob at the end of a bobbing display or alone as he approached the female. All eight males performed it in at least one test but only one male always courted using it. When this display was used, it usually immediately preceded an attempted neck grip (15 of 18 tests). This jiggle bob may be an important part of courtship and may be performed with greater regularity if the females showed signs of receptivity.

Of the seven video taped bobbing displays in courtship sequences of three males, only one was the signature pattern. The pattern of the rest could not be characterized. All four displays in the two courtships that ended in neck grips were four-legged push-ups with the tail lifted as the head bobbed up and the dewlap pulsed. This tail lift was a very common (28%) modifier in all courtship bobbing displays.

The overall frequency of all types of displays in courtship sequences by 8 different males in 33 tests was 0.35/minute which is about half that of a dominant male in an agonistic situation (0.66/minute). As was the case of the agonistic tests, the data can be combined because variance of display frequency between performances in different tests was relatively low (0.05). The frequency of bobbing displays with dewlap flashes were similar in premating and postmating displays (0.32 vs. 0.21) which was similar to that in agonistic encounters (0.23). There was both inter- (57%) and intra- (43%) individual variation in the use of the dewlap ($F = 1.3$, $p > 0.20$). The proportion of displays which were dewlap fanning displays were similar in courtship (0.15) and agonistic situations (0.14), but a higher proportion of the displays after mating (0.50) than before (0.10) were dewlap fanning (Fig. 7). Six of the seven complete matings, and none of the short matings, were followed by a dewlap fanning display, most of which had a distinctive erect posture (Fig. 8). But bobbing displays and further attempts to regain a neck grip followed one of the incomplete matings. Thus, bobbing displays may be predominantly a premating signal, and in this context fanning displays may be a signal of a successful copulation.

CONCLUSIONS

The male *Anolis sagrei* of this study show variability in both pattern and contextual use of displays. *Anolis sagrei* has only one species specific stereotypic pattern which may be used in every context. This signature display when used by males in the agonistic encounters was quite variable both in the total number of bobs and the number of bobs in each unit. In addition, the accompaniment of the dewlap extension was also variable; although, if it was used, it was always associated with one particular unit of the display, the

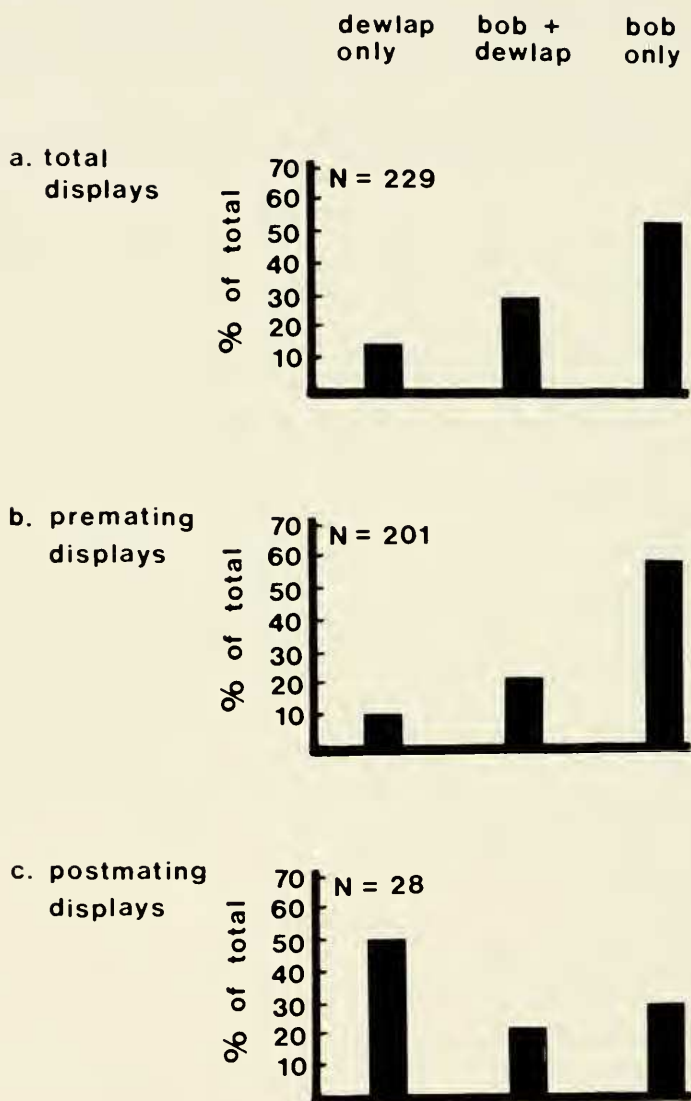


Figure 7. Frequency distribution of display types performed by males in courtship.

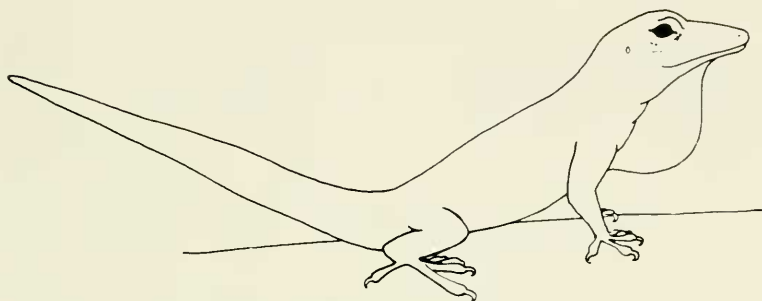


Figure 8. Typical post-copulatory display of dewlap fanning and erect posture.

long bob. This display is so variable that sometimes the signature pattern cannot be recognized. Video taped agonistic and courtship encounters showed that the species-specific signature pattern was used in almost all displays directed toward other territorial males, but was hardly or not at all recognizable in courtship displays.

The only displays which are consistent in their form and use are not species-specific. The jiggle bob, although not always performed in courtships of unreceptive females, was never seen in any other context. The display of rapid rhythmic bobs, shown by submissive males, was not performed by courting males and only rarely by territorial males, and then modified by a very aggressive posture. The dewlap fanning display was seen in all contexts but was used consistently after copulation with a distinct erect posture and may be associated with successful copulation. It has not been described as such for other species, but probably occurs in *A. carolinensis* (Crews, personal communication) and may be used by other anoles.

The color of the dewlap is also a species specific signal. But it may not be a symbol to aid species recognition as much as a means of emphasizing the bobbing display with the bright flash of color (Greenberg and Nobel, 1944; Williams and Rand, 1977). Dominant males in agonistic situations use the dewlap in bobbing displays significantly more than submissive males, but the dewlap is used for fanning displays at a significantly higher frequency by submissive males. Therefore, dewlap flashes alone may be less aggressive signals than when they accompany bobbing displays.

If the dewlap *per se* were being used as a species-specific signal, one might hypothesize an increase in its use in courtship. However,

fanning displays comprise a small proportion of premating displays, which is lower than its average use in other contexts, and the dewlap is used in bobbing displays at only slightly higher frequencies during courtship prior to mating than at other times. Therefore the two signals, the dewlap and the species-specific signature pattern, which one might expect to play a role in species recognition and female choice, are not particularly associated with courship, at least not when the animals are at relatively close range as they were in these tests.

Anolis sagrei originates from Cuba, an island with a very complex *Anolis* fauna (22–28 species, Williams, 1969). The stereotyped display pattern is more variable than one might expect with so many congeneric species needing reproductive isolation (Ruibal, 1967). Information to enable species recognition may be redundantly coded by many physical and behavioral characteristics (Williams and Rand, 1977). This seems to be the case with *A. opalinus* on Jamaica, which has no discrete display pattern even though it is sympatric with its two closest relatives, *A. garmani* and *A. grahami*. All three species have similar dewlap color and display structure but differ greatly in body size, shape, and color (Jenssen, 1979).

The signature display and increased use of the dewlap with the display are associated with territorial status in agonistic encounters. But neither shows an increase in use as the encounter escalates. The state of arousal and the willingness to escalate may be communicated by the modifiers of the displays, especially body posture and shape, and probably by the timing of the events. The more aggressive male of a pair was usually the first to erect his crests, engorge his throat, and laterally compress his body. Small shifts in posture or position in tense moments are probably also used as aggressive signals. Characterization of the behavioral repertoire of *A. sagrei* has been elusive (Ruibal, 1967) because of this subtlety.

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